Early hominins in north-west Europe: a punctuated long chronology?

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Abstract

In light of changing views regarding the identity and evolutionary positions of Europe's Lower Palaeolithic hominins, a re-consideration of the hominin occupation of North-West Europe from *c*. 1 million years ago (mya) to *c*. 400 thousand years ago (kya) is timely. A change in the scale and character of the overall European Palaeolithic record around *c*. 800-600 kya has been well documented and argued over since the mid-1990s. Hominin expansion into the European north-west, potentially from southern Europe, Africa or south-western Asia, has been linked to the introduction of a new lithic technology in the form of the biface. We evaluate three potential drivers for this northern range expansion: changing palaeo-climatic conditions, the emergence of an essentially modern human life history, and greater hominin behavioural plasticity. Our evaluation suggests no major changes in these three factors during the *c*. 800-600 kya period other than enhanced behavioural plasticity suggested by the appearance of the biface. We offer here a model of hominin occupation for north-west Europe termed the 'punctuated long chronology' and suggest that the major changes in the European Lower Palaeolithic record that occur at a species wide level may post-date, rather than precede, the Anglian Glaciation (marine isotope stage (MIS) 12).

Highlights

- European Lower Palaeolithic includes key shift in hominin distribution.
- Shift from below 45° north to broader range including higher latitudes.
- Changes in palaeoenvironmental conditions or hominin life history not key factors.
- Increasingly plastic behaviour may have enabled hominin range expansion.

1. Introduction

The hominin occupation of North-West Europe is a complex and important story for understanding hominin abilities to adapt to novel environments and the implementation of the plastic behaviours that were first developed on the savannahs of Africa and Eurasia (Dennell, 2003; Dennell and

41 Roebroeks, 2005; Grove, 2011; Potts, 2013). North-West Europe is important due to the unique
42 challenges that faced hominins within the higher latitude belt in terms of that region's distinctive
43 flora, fauna and seasonality. The earliest hominin occupation of Europe has traditionally been seen
44 through the long, short, and modified short chronologies (Carbonell et al., 1996; Dennell and
45 Roebroeks, 1996; Dennell, 2003; Roebroeks and van Kolfshoten, 1994; Table 1), recently enriched
46 through the Eurasian perspective (Dennell, 2004).

Model	**Long Chronology (Carbonell et al., 1996)**	**Short Chronology (Roebroeks and van Kolfshoten, 1994)**		**Modified Short Chronology (Dennell and Roebroeks, 1996)**
Summary	Europe occupied in the Early Pleistocene, and in some cases before *c*. 1.5 mya	"No undisputable proof for human occupation of Europe prior to about 500,000 years ago" (Roebroeks and van Kolfshoten, 1994: 500)		"Hominids might have occasionally moved into southern Europe well before 500,000 years ago, as and when conditions permitted" (Dennell and Roebroeks, 1996: 540)
Evidence				
Timeframe	**Before 780,000 years ago (pan-Europe)**	**Before 500,000 years ago (pan-Europe)**	**After 500,000 years ago (pan-Europe)**	**Before 780,000 years ago (Southern Europe)**
Archaeological signature	Small assemblages (typically 10s and 100s of artefacts)	Small series of isolated pieces selected from a natural pebble background	Large collections from excavated knapping floors with conjoinable material	Small assemblages (typically 10s and 100s of artefacts)
Context	Cave(?) and open-air sites (pan-Europe)	Disturbed secondary contexts	Primary context sites (fine-grained matrix)	Cave(?) and open-air sites (Iberia)
Assemblage character	Flake and pebble tools	Contested 'primitive' assemblages	Uncontested Acheulean and non-Acheulean	Flake and pebble tools

			industries	
Human Remains	Occasional	No human remains	Human remains common	Occasional

47

48 **Table 1:** Summarising the long, short and modified short chronologies, as originally proposed (Carbonell et al., 1996; Dennell and Roebroeks, 1996; Gamble,

49 1999; Roebroeks and van Kolfshoten, 1994).

The long and short chronologies have been hampered by the resolution and scale of the archaeological record and uncertainty whether evidence for hominin presence and absence in North-West Europe prior to 800 kya is a genuine behavioural pattern or the result of research and/or taphonomic bias (Roebroeks and van Kolfshoten, 1994). However, discoveries at a number of sites including Dmanisi, Georgia (Lordkipanidze et al., 2007); Orce and Atapuerca, Spain (Carbonell et al., 2005; Carbonell et al., 1995; Toro-Moyano et al., 2013); Pirro Nord, Italy (Arzarello et al., 2007); Pont-de-Lavaud and Lunery-Rosières, France (Despriée et al., 2011); and Happisburgh III, UK (Ashton et al., 2014; Parfitt et al., 2010) have been instrumental in challenging the notion of a hominin absence in Europe pre-800 kya. Happisburgh III has also challenged the notion of early hominin intolerance for harsh climatic conditions. There are however, still clear arguments to be made in regards to the sustainable nature of early forays substantially above the 45°N mark (MacDonald et al., 2012).

A related question concerns the increasingly complex role of *Homo antecessor* in the earliest human occupation of north-west Europe. It is *Homo antecessor* that has been put forward as one of the contenders for the pre-800 kya human presence at Happisburgh III (Ashton et al., 2014). Although their fossil evidence is limited to the Iberian Peninsula, it is possible that a series of short-lived dispersal events by this species above 45°N may have been the cause of the sparse archaeological record in Europe before 800 kya.

The pace and rhythms of early hominin dispersal in Europe are therefore varied and challenging to decipher. What is clear however is that hominin development must have occurred in conjunction with changes in climate and environment. It is the understanding of the specific climatic and environmental challenges to hominin survival in north-west Europe, and potential solutions to those challenges, which forms the focus of this paper.

2. How to survive Pleistocene North West Europe

Delays in the occupation of northern Eurasia, above *c*. 45°N, after the initial dispersals or range expansions of *H. erectus* (*s. lato*) beyond Africa, suggest that a sustained presence in the north presented significant new challenges to Lower Palaeolithic hominins. Modern ethnographic, ecological and climatological studies would suggest that those challenges were principally increased seasonality, lower mean temperatures, contrasting oceanic and continental zones, reduced plant food resources, and more dispersed and clustered animal food resources (Gamble, 1986; Hosfield, 2016; Kelly, 1995; Roebroeks, 2001, 2006). How might these challenges be met? The 'solutions' can be grouped into two broad categories: firstly, increased animal food contributions to the diet, with implications for the reliability of foraging strategies, the sizes of territories and the knowledge required of landscapes and resources, hominin mobility, social group organisation, and technology. Secondly, enhanced insulation, which can be cultural (encompassing some or all of pyrotechnology, whether managed or opportunistic, 'clothing' or other forms of body covering, and shelter) and/or physiological (e.g. elevated BMR [basal metabolic rate], increased muscle mass, body hairs, elevated brown adipose tissue levels; but *cf*. Aiello and Wheeler, 1995; Aiello and Wheeler, 2003).

These 'solutions' can be most easily described as changing hominin behaviours (i.e. increasingly efficient dietary and insulation strategies). Yet our clearest material insights into hominin behaviour (the lithic record) shows relatively little evidence for major changes across the duration of the Lower Palaeolithic (Klein, 2000), and while Acheulean technology may be absent from the repertoire of the earliest Europeans, it already had a long history in Africa and western Asia by the time of those first dispersals into the Mediterranean. We therefore propose three other potential forms of change which may also be key factors in the pre-/post-800kya settlement patterns in northern Eurasia (Table 2), and ~~will~~ explore these within a European framework: (i) changes in the palaeoclimate and palaeoenvironmental context; (ii) changes in hominin life history; and (iii) changes in behavioural plasticity.

Period	Chronology	Sites
Later Early Pleistocene	*c*. 1.3–0.78mya	Happisburgh III, Lunery-Rosières, Pont-de-Lavaud
Early Middle Pleistocene	*c*. 0.78–0.5mya	Abbeville, Boxgrove, Happisburgh I, High Lodge, Kärlich G, La Genetière, La Noira, Miesenheim, Pakefield, Warren Hill
Later Middle Pleistocene	*c*. 0.5–0.3mya	Beeches Pit, Bilzingsleben, Clacton, Hoxne, Schöningen, Soucy, Swanscombe,

Table 2: Key chronological phases and selected northern European sites (after Ashton, 2015).

2.1 The palaeoenvironmental context

To what extent may changing palaeoclimatic and palaeoenvironmental conditions underpin the changes in scale in the northern European settlement record? Such arguments have been widely explored. Turner (1992) emphasised the changing large carnivore guild around 500kya and the gradual emergence of the 'mammoth steppe' after MIS 12 (Guthrie, 1990), linked to the changing length of glacial/interglacial cycles during the Mid-Pleistocene Transition (Head and Gibbard, 2005). However, many of these models have tended to primarily emphasise long-term trends. While these are undoubtedly important, the emphasis in this paper is upon the daily, seasonal and yearly challenges to hominins: e.g. low winter temperatures, the degree of seasonality, short-term climatic shifts (e.g. on decadal scales), the diversity or homogeneity of habitats at a local scale, and the condition and availability of plant and animal foods across the seasons. These are increasingly well understood through micro-fauna (e.g. Coope, 2006a), palynology, and the multi-disciplinary investigations of key sites (Bigga et al., 2015; García and Arsuaga, 2011; Parfitt et al., 2010; Parfitt et al., 2005; Rodríguez et al., 2011; Urban and Bigga, 2015), enabling us to consider the nature of the hominin life experience 'on the ground'. We are taking this approach not least because while the MIS record emphasises the increasing stability, length, marked oscillations and decreasing

121 temperature of European glacial/interglacial cycles during the Middle Pleistocene, intra-site records
122 reveal that stability is less apparent at the sub-stage scale (Ashton et al., 2008a; Urban and Bigga,
123 2015) and may also have been less apparent at the scale of a hominin lifetime too. The key question
124 is can we see clear evidence for a shift in hominin environments across the *c*. 800-600kya boundary
125 that might favour a more sustained northern presence?
126
127 **2.2 Changes in hominin life history**
128 Changing life history may be a second key factor. The current European fossil record suggests an
129 apparent species contrast pre- and post-800-600kya, with *H. antecessor* (Carbonell et al., 1995)
130 replaced by *H. heidelbergensis* (Stringer, 2012) across the chronological division. It may well also be
131 significant that the Sima de los Huesos fossils, dating to *c*. 430kya, are now argued to be early
132 Neanderthals, or closely related to the latter's ancestors (Meyer et al., 2016b). Why might life
133 history be significant? The modern human life history stages (childhood, juvenile, adolescence,
134 adulthood) are associated with the unusual collection of traits which characterise humans:
135 prolonged gestation, growth and maturation, extremely short inter-birth intervals, helpless
136 newborns, a short period of breastfeeding/early weaning, extended offspring dependency, an
137 adolescence growth-spurt, delayed reproduction, and the menopause (Bogin and Smith, 1996;
138 Schwartz, 2012).
139
140 Of particular importance to the occupation of the north may be the emphasis in the human model of
141 early weaning: this strategy places infants at risk, as they are unskilled at finding appropriate foods
142 (of sufficient high quality to fuel brain growth, but also suitable for small, deciduous teeth), are
143 essentially defenceless, and can be competing with other adults (Aiello and Key, 2002; Kennedy,
144 2003). It therefore has notable dietary strategy implications, but it also has significant implications
145 for infant care. Since early weaning is associated with shorter inter-birth intervals, other forms of
146 childcare are required for the 'weanlings', in order to avoid excessive DEE (daily energy expenditure)

147 loads on the large-bodied and large-brained *Homo* females (i.e. normal DEE + gestation/lactation +
148 nursing of 'weanlings'; Aiello and Key, 2002). This alloparenting can come from grandmothers (e.g.
149 Hawkes et al., 1998) or older siblings, or in the form of increased male provisioning.
150
151 As noted above, a change to a fully modern life history would therefore bring costs, but the addition
152 of an adolescence stage can also bring specific opportunities to improve selective fitness. In a
153 broader context, extended growth development would enable socialisation – learning the 'rules' of
154 social life (e.g. hierarchies of food access, recognising the moods and emotions of individuals), made
155 complicated both by larger communities, as predicted by neocortex size and the social brain
156 hypothesis (e.g. Gamble et al., 2014), and perhaps also by periods of individuals' absences, arising
157 from dispersed resource distributions and social fission-fusion in the seasonal mid- and high-
158 latitudes (Couzin and Laidre, 2009). Kennedy (2003) has argued that adolescence would enable
159 youngsters who were close to maturity to observe and participate in the social, sexual and infant-
160 care practices that are critical to success in adulthood. Bogin and Smith (1996) have similarly
161 emphasised adolescence as a period when parenting skills could be practiced, perhaps resulting in
162 the greater survival of their own offspring later in life. MacDonald (2007) has stressed the knowledge
163 demands of a hunting life, from animal behaviour and their signs, to animal-animal and animal-plant
164 relationships, to the topography, vegetation and seasonality of the environment. Foraging for plant
165 resources, while stationary, would also require a diverse set of ecological knowledge. Adolescence
166 would offer an opportunity to develop much of this base-line knowledge, and the associated skills –
167 not least because the nature and content of learning will vary with age, as both the mind and the
168 body develops (MacDonald, 2007). Thus a modern human model of life history might produce sub-
169 adults and adults with the skills and knowledge to meet the social, ecological and technological
170 challenges of the north.
171

We can discuss life history and its evolution amongst extinct hominins (Fig. 1) because of the evidence for strong correlations between a range of life history traits: brain size, body size, age at sexual maturity, age at first birth, gestational length, lifespan, and dental development (Kennedy, 2003). The critical question from a European Lower Palaeolithic perspective would therefore seem to be: can we detect any evidence for adolescence in particular, and a truly human model of growth and development in the hominins of the late Early Pleistocene and early Middle Pleistocene?

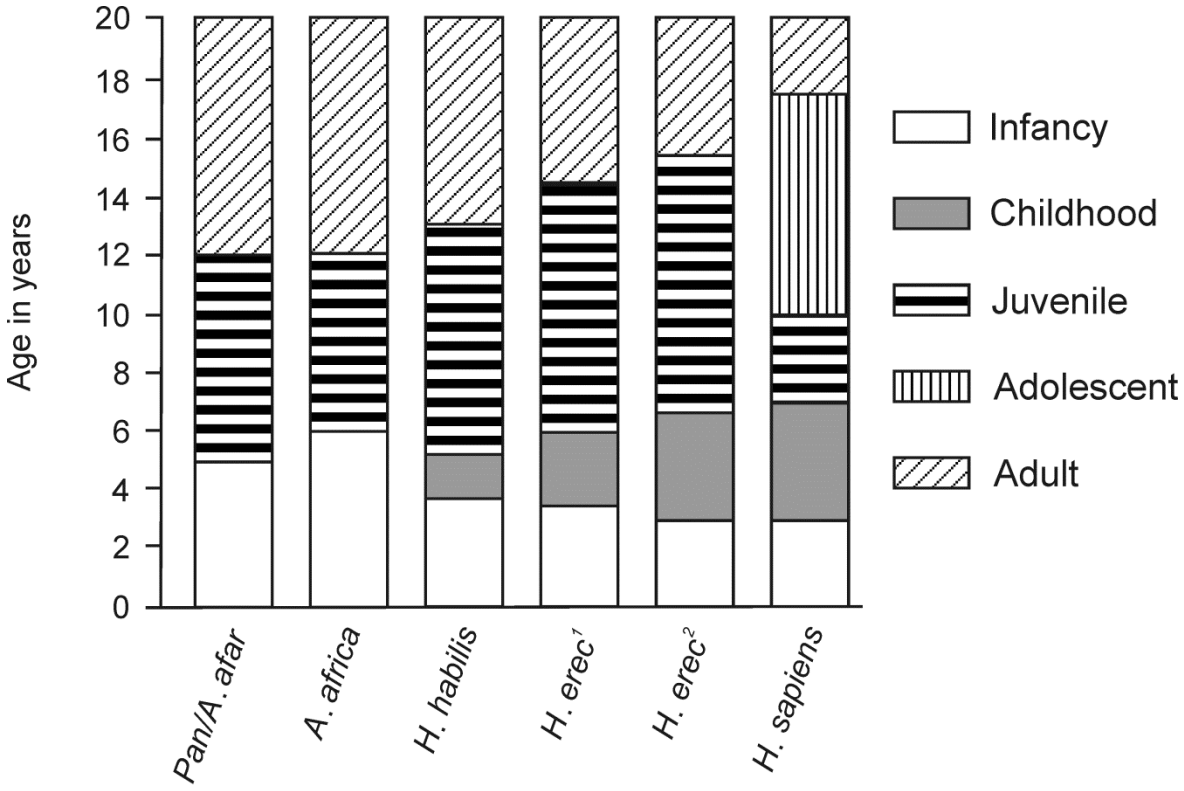


Fig. 1: Inferred life history stages for selected hominin species (Bogin, 1999: fig. 4.9). H. erec.-1 = early *H. erectus* (adult brain sizes of 850-900cc); H. erec.-2 = late *H. ~~omo~~ erectus* (adult brain sizes upto 1100cc); A. afar = *A. afarensis*; A. Africa = *A. africanus*.

2.3 Changes in behavioural plasticity

In addition to hominin genotypic adaptations to the north-west European palaeoclimatic and palaeoenvironmental conditions (although some traditionally considered "cold-adapted" hominin

187 traits have recently been questioned (e.g. Rae et al., 2011) hominin range expansion must also have
188 been characterised by phenotypic adaptations to external factors. Archaeologically speaking it is the
189 phenotypic adaptations of behaviour that are the most visible indicators of behavioural plasticity.
190
191 It has been suggested for some time that organisms that are both mobile and long-lived are less
192 likely to adapt to local conditions through the selection of genetically based traits (Potts, 1998, 2013;
193 van Schaik, 2013). In effect, the suggestion is therefore that when such organisms encounter
194 variable climatic conditions they are more likely to adapt to those conditions at a phenotypic level
195 rather than a genotypic one (van Schaik, 2013). However, it would also appear that the plastic
196 behavioural strategy may fail if local environments change too rapidly (Van Buskirk, 2012; van
197 Schaik, 2013). This in turn suggests that behavioural plasticity can only carry a species so far in its
198 effectiveness in negotiating novel or rapidly changing environments.
199
200 Another important aspect to consider in regards to behavioural plasticity are the links to cognitive
201 capacity and brain size (van Schaik, 2013). From a primate perspective behavioural plasticity derives
202 from learning through mental mechanisms linked to varying degrees of cognitive complexity
203 (Shettleworth, 2010). These processes have been tightly linked to brain size and therefore suggest
204 that behavioural plasticity should be included in the costs of supporting larger brains (van Schaik,
205 2013). Therefore, it follows that the degree of behavioural plasticity present within an organism may
206 correspondingly be limited by overall brain size. Within the hominin fossil record it has been
207 suggested previously that there are recognisable step changes in hominin brain size (Maslin et al.,
208 2014; McNabb and Cole, 2015; Shultz et al., 2012; Fig. 2) at *c*. 1.8mya, 1mya, 400–200kya, and
209 100kya, which punctuate periods of stasis in hominin brain expansion. Shultz et al. (2012) further
210 highlight that the increase in hominin brain size *c*. 400–200 kya may be as a result of migrating
211 hominin species into Eurasia as the step changes are not mirrored in Africa. However, from Figure 2

it could be cautiously suggested (based on the limited sample available) that there may also be an increase in hominin brain size within *Homo heidelbergensis c*. 800–600 kya.

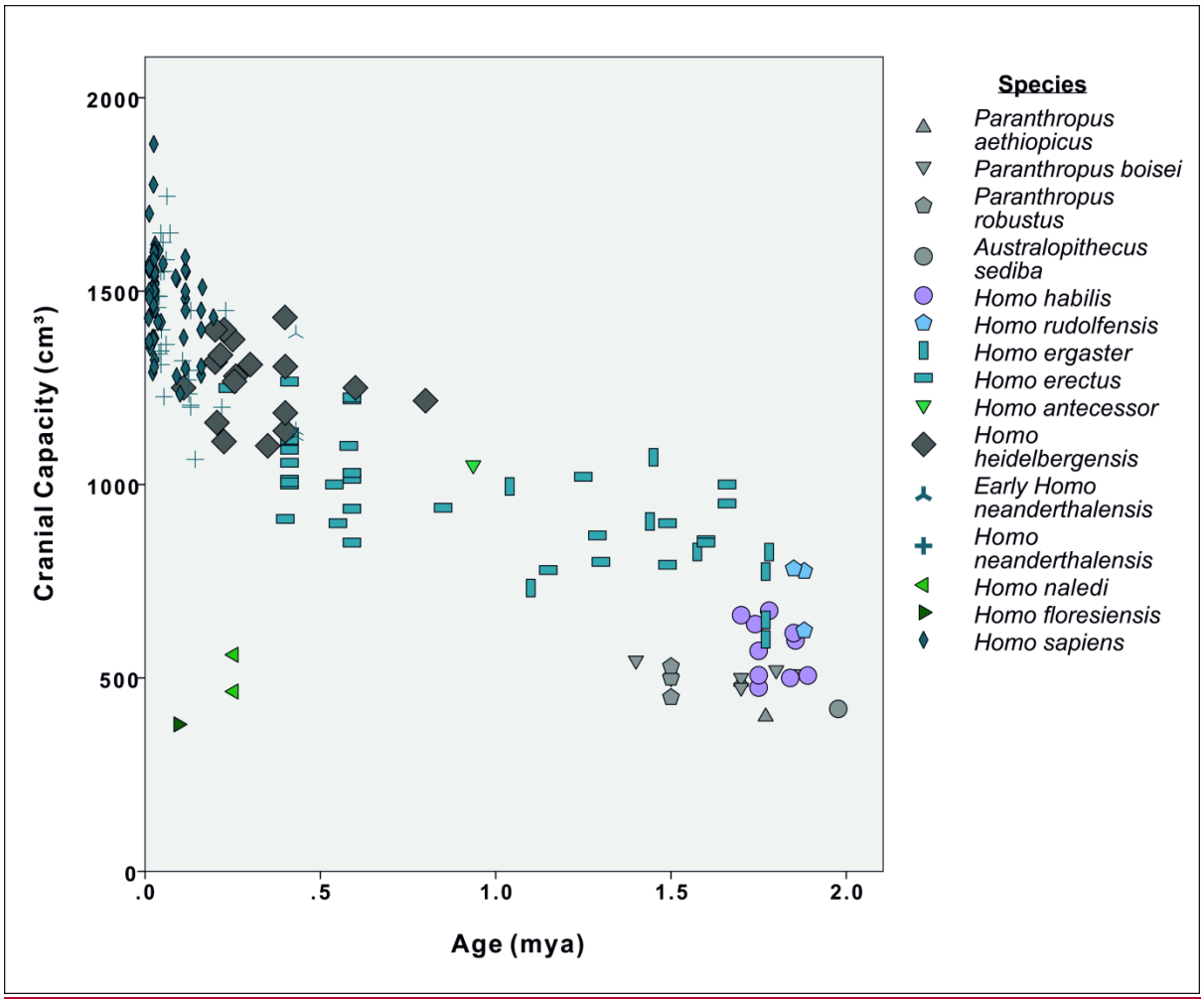


Fig. 2: ~~Showing h~~Hominin cranial volumes (cm^3) ~~at a~~over the last 2myr ~~a (A) and 1mya (B) scale. The fossil specimens and species are divided by location~~ (data after Berger et al., 2015; Brown et al., 2004; Shultz et al., 2012; Thackeray, 2015).

Indeed, if behavioural plasticity and brain size are linked then there is a possibility that a more sustained hominin presence in north-west Europe may require a threshold level of both plasticity and brain size. Therefore, examining the fossil and behavioural signatures of Pleistocene hominin activity in north-west Europe against the context of changing environmental conditions should

provide some insight as to the degree of plasticity present, and whether an increase in behavioural plasticity coinciding with an increase in brain size is significant enough of an advantage to lead to a more sustained hominin presence after *c*. 600kya.

3. Discussion

Following the three broad themes presented above, we will now examine and review the evidence for each.

3.1 Palaeoenvironment

Kahlke et al. (2011) argue that 1.2–0.9mya (the late Early Pleistocene) was a period of less uniform climate cycles, varying in both duration and intensity. These climate cycles would have been associated with new mammal communities, increasing varieties of habitats, large riverine systems, and relatively mild and humid conditions, especially in the Mediterranean and the west. As Kahlke et al. (2011) have previously argued, these conditions seemingly favoured the expanding occupation of the Mediterranean zone at sites such as Barranco León and Fuentenueva-3 (Orce), Sima del Elefante (TE9), Pont-de-Lavaud, Lunery-Rosières, Le Vallonnet III (although the character of the lithic assemblage has been strongly critiqued; Roebroeks and van Kolfshoten, 1994) and Monte Poggiolo (Leroy et al., 2011), while dispersal into the north was restricted to favourable interglacials of low seasonality and high habitat diversity, for example at Happisburgh III (Parfitt et al., 2010). By contrast, the period after 0.9mya was increasingly controlled by 100kyr periodicity, with longer and relatively stable climatic intervals, progressive temperature decline and increasing aridity, marked oscillations between highly contrasting landscapes, greater seasonality, and increasingly specialized mammal communities (Kahlke et al., 2011: 1389). These changes ~~become~~ became especially marked after *c*. 500kya (Berger and Loutre, 1991; Lisiecki and Raymo, 2005). Perhaps critically from the perspective of hominin distribution and dispersal, these changes were accompanied by regional shifts in characteristic habitat types (Table 3).

Region	Prevailing habitats (inferred from large mammal communities)				
Apennine Peninsula	High variety of open / forested habitats		Open woodland / steppe		
Iberian Peninsula	Open savannah / lightly forested habitats		Open woodland, tree savannah / steppe		
Western Europe	High variety of open / forested habitats		Woodland / steppe		Variety of open to forested habitats
Northwest Europe	Woodland		Woodland with open patches / mixed habitats		Steppe / woodland
Central Europe	High variety of open / forested habitats		Steppe / woodland with open patches		Steppe-tundra / woodland
Eastern Europe	High variety of forest steppe / open steppe habitats		Open steppe / forest steppe		Steppe-tundra / woodland
Chronology (mya)	1.2	1.0	0.8	0.6	0.4

Table 3: Prevailing habitat characteristics in Europe over the last 1.2mya (re-drawn after Kahlke et al., 2011: Fig. 6).

What might these regional differences have meant in terms of hominin life on the ground? Can we see any evidence of significant change over time? Offering a northern Iberian perspective from Atapuerca, Rodríguez et al. (Rodríguez et al., 2011) have argued for an absence of harsh conditions

257 across the long time-span of the Sima del Elefante, Gran Dolina, and Galería sites. This was based on
258 a wide range of evidence: small vertebrates (amphibians, squamates and small mammals), large
259 mammals, and vegetation (Table 4). Rodríguez et al. (2011) conclude that these prevalent temperate
260 conditions may be associated with a continuous early hominin presence prior to *c*. 0.5mya, and
261 perhaps reflect a *H. antecessor* preference for warmer, less variable conditions (see also Agustí et al.,
262 2009).
263
264 So what changes in terms of hominin habitats? The answer from south-western Europe, using
265 Atapuerca as a case study, may be not much. Rodríguez et al.'s (2011) admittedly tentative
266 environmental reconstructions (Table 4) suggest little change between the Early and Middle
267 Pleistocene, while Garcia & Arsuaga's (2011) analysis of the Sima de los Huesos evidence suggests a
268 savannah-like open woodland, dating to *c*. 430kya on the basis of the most recent dating (Arnold et
269 al., 2014). But what is the view from the north?

Evidence	Key Patterns (Early & Middle Pleistocene)	
Small vertebrates	• Significant woodland component in herpetofauna • Small mammals suggest moist, open habitats	
Large mammals	• All of temperate affinity • None unequivocally indicating cold or arid environments	
Vegetation	• Continuous presence of Mediterranean taxa & mesic trees • One possible cold steppe landscape phase	
Palaeotemperature (amphibian & squamate assemblages)	• Always warmer than Burgos today • "Cold"/"warm" period differences of only *c*. 2°C	
Annual precipitation	• 750mm (dry)–1049mm (humid), compared to *c*. 570mm in present	
Environment types	**Early Pleistocene** • Mediterranean open woodland • Open woodland and steppe • Open arid (?) • Open woodland and moist meadows • Temperate open woodlands and meadows with lagoons	**Middle Pleistocene** • Humid temperate open woodland • Mediterranean open woodland • Moist meadows with scattered trees • Open woodland and meadows • Steppe

Table 4: Inferred environments at Atapuerca in the Early and Middle Pleistocene (after Rodríguez et al., 2011: table 9).

There is evidence of a tolerance of cooler conditions as a whole (e.g. Hosfield, 2011: table 6), gained from palaeotemperature estimates and environmental descriptors from a range of key northern

sites with evidence of hominin activity. These offer a valuable perspective on possible changes in hominin tolerances and/or preferences in northern Europe across the *c*. 800-600kya 'boundary' (Table 5). Summer and winter palaeo-temperatures reveal no major changes across the boundary as a whole, although there is perhaps some evidence for slightly harsher conditions in the MIS 13/15 sites, in contrast to the MIS 11 sites and Pakefield. This might be significant, and slightly counter-intuitive, as MIS 13 sees a marked increase in the number and size of sites across northern Europe (e.g. examples in Tables 5 & 6, plus Warren Hill, Highlands Farm, Valdoe, Kent's Cavern, Abbeville, Miesenheim, and Kärlich G; see also Ashton, 2015).

Site	**T_{min} (°C)**	**T_{max} (°C)**	**Evidence[1]**	**Age (MIS)**	**Source**
Early Pleistocene					
Happisburgh III (Bed E)	-3 – 0	+16 – ±18	Coleoptera	Late 25 or late 21	(Ashton and Lewis, 2012; Parfitt et al., 2010)
Early Middle Pleistocene					
Pakefield (Bed Cii–Ciii)	-6 – +4	+17 – ±23	Coleoptera	17 or later 19	(Ashton and Lewis, 2012; Coope, 2006b)
Boxgrove (Unit 4c & Freshwater Silt Bed ≈ Units 4b & 4c)	-4 – +4	+15 – ±20	Ostracods (MOTR) & Herpetofauna (MCR)	13	(Ashton and Lewis, 2012; Holman, 1999; Holmes et al., 2010)

Happisburgh I (Organic Mud)	-11 – -3	+12 – ±15	Coleoptera	13?	(Ashton and Lewis, 2012; Coope, 2006b)
High Lodge (Bed C1)	-4 – +1	+15 – ±16	Coleoptera	13?	(Coope, 2006b)
Waverley Wood (Channel 2, Organic Mud)	-	+10 – ±15	Coleoptera	13 or 15	(Coope, 2006b; Shotton et al., 1993)
Brooksby (Redland's Brooksby Channel)	-10 – +2	+15 – ±16	Coleoptera	13 or 15	(Coope, 2006b)
Later Middle Pleistocene					
Barnham (Unit 5c; HoII)	-	+17 – ±18	Herpetofauna	11c	(Holman, 1998)
Hoxne (Stratum D[5]; HoIIIa[6])	-10 – +6	+15 – ±19	Coleoptera	11c	(Ashton et al., 2008a; Coope, 1993)
Bilzingsleben II	-0.5 – +3	+20 – ±25	Mollusca & ostracods[2]	11	(Mania, 1995; Mania and Mania, 2003)
Schöningen 13 II-4	-4 – -1	+16	Mollusca & ostracods	9	(Urban and Bigga, 2015)
Present Day Comparisons					

East Anglia (present day)[3]	-0.7 – +6.9	+14.2 – + 18.0	-	-	-
Bilzingsleben (present day)[4]	-3.3 – +2.0	+12.4 – +22.7	-	-	-

Table 5: Winter and summer temperature estimates for Early and Middle Pleistocene British and German sites (with selected present day equivalents for reference). [1]Sensitivity tests on coleoptera-based MCR procedures suggest that winter temperature estimates are usually too warm (Pettitt and White, 2012: 35). [2]The specific source of the palaeo-temperature estimates is not stated, but the fauna includes molluscs and ostracods; [3]East Anglian data based on Met Office annual mean seasonal temperatures (1910–2016; http://www.metoffice.gov.uk/pub/data/weather/uk/climate/datasets/Tmean/date/East_Anglia.txt); [4]Bilzingsleben data based on Deutscher Wetterdienst (German Weather Service) monthly mean January and July temperatures (1951–2017; Erfurt-Weimar station; https://www.dwd.de/DE/leistungen/klimadatendeutschland/klarchivtagmonat.html)

Site	**Palaeoenvironmental description**	**Age (MIS)**	**Source**
Early Pleistocene			
Pont-de-Lavaud	Closed deciduous forest; warm, wet climate	30	(Messager et al., 2011)
Happisburgh III (Unit C)	Cool temperate; heathland & coniferous forest	Late 25 or late 21	(Ashton and Lewis, 2012)
Happisburgh III (Units D & E)	Cool temperate; dominated by coniferous forest	Late 25 or late 21	(Ashton and Lewis, 2012)

Early Middle Pleistocene			
Pakefield (Units Aiv–Ciii)	Mediterranean-type climate; marshy ground with reed-beds & alder carr, surrounded by deciduous forest	17 or later 19	(Ashton and Lewis, 2012)
Happisburgh I (Organic Mud–Organic Silt Sand)	Cool climate; marshy edge of slow-flowing river, with surrounding coniferous forest	13?	(Ashton and Lewis, 2012)
High Lodge (Units B2–C2)	Cool-temperate climate; marshy ponds, heath & grassland on river floodplain, surrounded by pine & spruce forest	13?	(Ashton and Lewis, 2012)
Boxgrove (Unit 4b)	Coastal mudflats, with occasional drying out & spread of grassland	13	(Ashton and Lewis, 2012)
Boxgrove (Unit 4c & Q1B pond deposits)	Temperate climate, with cooler winters than present; grassland, scrub & mixed woodland, with spring-fed pools	13	(Ashton and Lewis, 2012)
Boxgrove (Unit 8)	Interstadial environment	Later 13–early 12	(Ashton and Lewis, 2012)
Boxgrove (Unit 11)	Periglacial, with ameliorations in climate	Later 13–early 12	(Ashton and Lewis, 2012)
Later Middle Pleistocene			
Bilzingsleben II	Fully temperate, with subcontinental influences; mixed oak woodland & shrub associations, alternating with steppe meadows	11	(Mania and Mania, 2003)
Barnham (Unit 5c;	Temperate climate; mix of grassland &	11c	(Ashton and

HoII)	deciduous woodland on edge of slow-flowing river		Lewis, 2012)
Beeches Pit (Unit 4; HoIII)	Fully temperate environment; spring-fed pools with deciduous woodland	11c	(Ashton and Lewis, 2012)
Beeches Pit (Unit 3b; HoIIb–c)	Temperate climate; shallow to stagnant pools with calcareous grassland and surrounding open woodland	11c	(Ashton and Lewis, 2012)
Hoxne (Unit B1)	Cooler temperatures (*cf*. units D & E); probable birch & pine forest; some grassland areas	11a	(Ashton and Lewis, 2012)
Swanscombe (Lower Loam; HoIIb–c)	Grassy floodplain with shallow pools & occasional flooding; mixed oak forest nearby, with hazel & alder	11c	(Ashton and Lewis, 2012)
Schöningen 13 II-4	Mosaic swamp, with reed-like and sedge vegetation; regional context: highly continental dry steppe/open forest; tree taxa dominated by pine & birch	9	(Stahlschmidt et al., 2015; Urban and Bigga, 2015)

298

299 **Table 6**: Palaeoenvironmental reconstructions for Early and Middle Pleistocene British sites and
300 German sites.

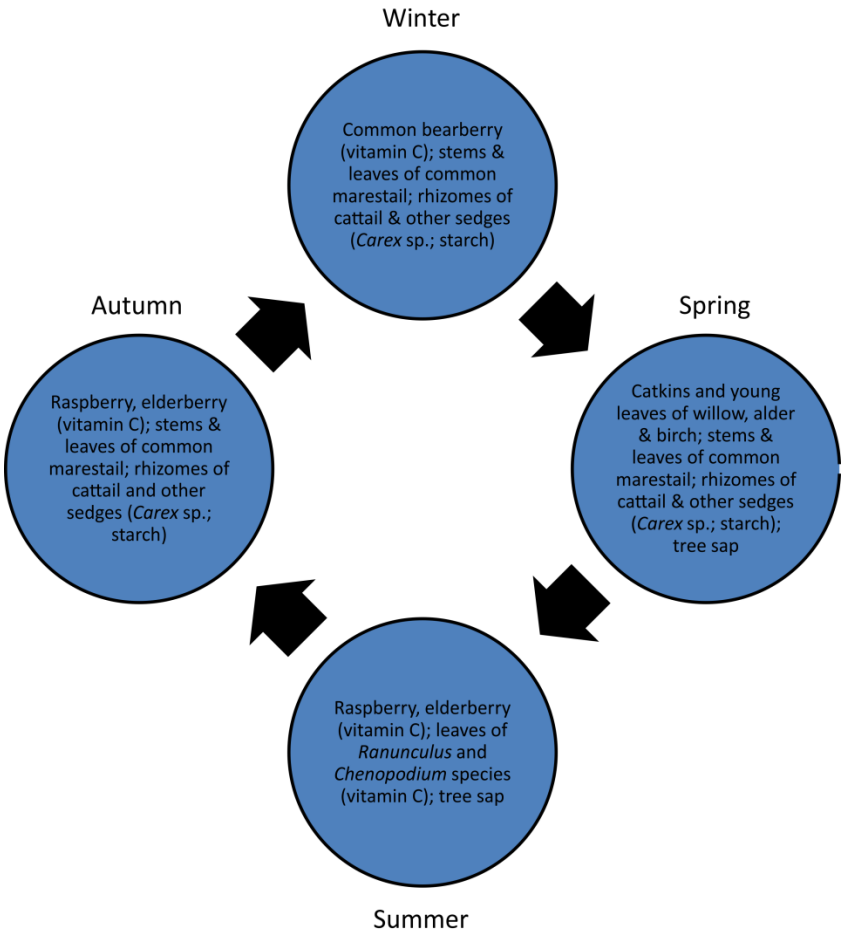
301

302 The general trend after MIS 13 is towards full or cool-temperate environments, mixing deciduous or
303 coniferous woodland with open grass and/or heathland, and water sources (Table 6). As Bigga et al.
304 (2015) have noted at Schöningen, such environments provide a diverse range of potential plant
305 foods, meeting both nutritional (e.g. vitamin C in pine and birch bark, berries of common bearberry,
306 European elder, raspberry, and leaves of *Ranunculus* and *Chenopodium*) and seasonal needs (Figure

307 3). Evidence of animal butchery also suggests few changes in preferred prey across the *c*. 800-600kya

308 boundary, or in comparison between northern and southern Europe (Table 7).

309



310

311 **Figure 3:** Seasonal variations in selected potential plant food sources identified at Schöningen 13 II-4

312 (Bigga et al., 2015).

313

Period	**Species**	**Butchery Evidence**	**Sites**
Early Pleistocene	*Bison* sp. *B. menneri* *B. voigtstedtensis* *C. elaphus* *C. s.l. nestii vallonnetensis*	Defleshing; disarticulation; dismemberment; evisceration; filleting; skinning	Gran Dolina TD6 (Saladié et al., 2011) Sima del Elefante (Huguet et al., 2013)

	Cervid sp. *Cercopithecidae* *Eucladoceros* *Equus sp.* *Hippopotamus* *S. etruscus* *S. hundsheimensis* *U. dolinensis* *V. praeglacialis*		
Early Middle Pleistocene	*Bos* or *Bison* sp. *C. capreolus* *C. elaphus* *E. ferus* *S. hundsheimensis* *U. deningeri*	Cut-marks; defleshing; dismemberment; filleting; marrow bone breakage; skinning	Boxgrove (Bello et al., 2009; Parfitt and Roberts, 1999) Happisburgh I (Ashton et al., 2008b) Westbury (Andrews and Ghaleb, 1999)
Later Middle Pleistocene	*Bos* or *Bison* sp. *C. elaphus* *E. ferus*	Boning; cut-marks; defleshing; dismemberment; filleting; marrow bone breakage; skinning	Barnham (Parfitt, 1998) Schöningen (Van Kolfschoten et al., 2015a; Voormolen, 2008) Hoxne (Stopp, 1993)

Table 7: European sites with butchery evidence.

What is perhaps more noticeable are the conditions at the Early Pleistocene sites of Happisburgh III and Pont-de-Lavaud, and at the MIS 17/19 site of Pakefield. The latter two sites both support a model of temporary northern excursions in line with favourable conditions. As other authors have previously noted (Parfitt et al., 2010), Happisburgh III stands out in the pre-800-600kya record, albeit within a very small sample of early northern sites.

Overall, combining general palaeo-environmental trends and the conditions at hominin sites suggests that the post-800-600kya expansions in the occupation of the north occur at an intuitively odd time – before the favourable MIS 11 interglacial but after the milder conditions of the later Early Pleistocene.

3.2 Life history

Turning away from environmental conditions, can we detect any evidence for childhood and adolescence, and a truly human model of growth and development, in the European Lower Palaeolithic? Of critical importance in beginning to resolve this question for Europe has been the *H. heidelbergensis* and *H. antecessor* fossil material from the Sima de los Huesos and Gran Dolina localities at Atapuerca (Bermúdez de Castro et al., 1997; Carbonell et al., 1995; these analyses pre-dated the recent re-attribution of the Sima de los Huesos material as possible early Neanderthals). Initial analysis of the dental material from TD-6 hominins 1 & 3 and Sima hominin 18 suggested that both European species are similar to modern humans in their dental development, implying both prolonged maturation and new life history stages (childhood and adolescence; Bermúdez de Castro et al., 2003), although *H. antecessor* is not as derived in some respects (e.g. delayed M3 calcification; Bermúdez de Castro et al., 1999). By extension that would also suggest relatively short birth intervals, high rates of postnatal brain growth, extended offspring dependency, marked adolescent growth spurt, and delayed reproductive cycles. Expanded analysis of enamel formation rates for various species of *Homo* also suggested prolonged dental growth in *H. antecessor* and *H.*

343 *heidelbergensis* (Ramirez Rozzi and Bermudez de Castro, 2004). Although their mean crown
344 formation times were concluded to be shorter than in Upper Palaeolithic–Mesolithic *H. sapiens*
345 samples, they were slower than those of Neanderthals, whose crown formation was estimated to be
346 15% quicker than modern humans. The data also suggested only slightly slower growth rates in *H.*
347 *heidelbergensis* (n=106; 21 individuals) compared to *H. antecessor* (n=8; 4 individuals; *ibid*: fig. 1).
348
349 However, these interpretations have been challenged to some extent by Robson and Wood (2008),
350 who have argued that *H. antecessor's* crown formation rates are not modern human-like (although
351 the tooth eruption timings are). They also noted that the crown formation rates of *H.*
352 *heidelbergensis* are more akin to *H. antecessor* than modern humans, a view supported by Rozzi &
353 Bermudez de Castro's data (2004: fig. 1). Contrasts with *H. sapiens* are also evident in Neanderthals'
354 more rapid dental development patterns (Ramirez Rozzi and Bermudez de Castro, 2004; Smith et al.,
355 2007), although suggested differences between those two species' overall rates of growth have
356 recently been challenged (Rosas et al., 2017). Overall Robson and Wood (2008) conclude that life
357 history shifts are likely to have been piece-meal (with body mass shifts pre-dating dental
358 developments; see also Krovitz et al., 2003), and also that dental development rates and timings do
359 not always correlate well with other life history variables.
360
361 These various models and data suggest that European Lower Palaeolithic hominins, whether *H.*
362 *antecessor* or *H. heidelbergensis*, are likely to have adopted at least a human-like model of
363 reproduction, growth and development, although childhood may not have been as prolonged as in
364 *H. sapiens*. However, it is worth considering whether life history may have become more human-like
365 with *H. heidelbergensis* (i.e. more prolonged maturation and more extended childhood and
366 adolescence stages), given the overlaps in endocranial volume between *H. sapiens*, *H.*
367 *neanderthalensis* and *H. heidelbergensis*, but not *H. antecessor* (Robson and Wood, 2008: fig. 6), and
368 the delayed M3 calcification and long I2 and C crown formation times in *H. antecessor* (Bermúdez de

Castro et al., 2003; Bermúdez de Castro et al., 1999). As noted above the human life history pattern offers the opportunity to learn skills and experiences that may have been critical in the seasonal latitudes of Europe (e.g. the extended practice argued to be required by prepared platform techniques; Stout et al., 2014). But differences between *H. heidelbergensis* and *H. antecessor* are likely to have been relatively small and it is not immediately obvious as to how and why small extensions in the childhood and adolescence stages, and other associated life-history changes, would facilitate the post-600kya expansion in northern Europe. In many ways, the suggested appearance of an adolescence stage in *H. antecessor*, and perhaps also *H. erectus* (Krovitz et al., 2003; but *cf*. Bogin and Smith, 1996, and Fig. 1) looks more significant, and may well relate to the earlier, first excursions into southern Europe.

3.3 Behavioural plasticity

Within the Lower Palaeolithic record, the biface represents a shift to a multi-functional tool that is easily transportable and adaptable (through resharpening and reworking) to a variety of situations (Moncel et al., 2015). There are a range of additional behavioural and cognitive changes that biface manufacture represents, including indications of greater planning depth, not only in tool production, use and curation, but also a more liberated attitude to landscape use and resource acquisition that potentially underpinned an expansion in group size and more complex group dynamics (Gowlett et al., 2012). Much of these additional bonuses may come from the acquisition of a sustained ability for abstract thought at a species level (Cole, 2015a; Cole, 2015b) contributing to a greater degree of sustained behavioural plasticity as brain sizes increase (Fig. 2). Therefore, tracking the earliest appearance of biface sites in north-west Europe could provide a useful insight into hominin behavioural changes. We follow Ashton (2015) in associating the bifaces of north-west with *Homo heidelbergensis*, as demonstrated at sites such as Boxgrove and Arago (Moncel et al., 2015).

394 Moncel et al. (2015) have produced an excellent review of biface manufacture in north-west Europe
395 from *c*. 700–600kya which suggests a more extensive biface presence in north-west Europe from
396 500kya (Table 8).

Age (MIS)	Contexts	Raw Materials	Characteristic Biface Morphology	Additional Flake Tools	Sites
17-13	Diamicton; fluvial gravel; fluvial sand; fluvial silts; lagoonal silts; palaeosol	Andesite; siliceous; flint; quartzite	Pointed (incl. crude forms); ovate; biface-cleaver; cordiforms	Denticulates; notches; scrapers	Boxgrove (Q1B); Brandon Fields; Happisburgh I; High Lodge (Bed E; Sands & Gravels); La Noira; Maidscross Hill; Warren Hill; Waverley Wood
12-10	Gravel; slope deposit; fluvial sand; fluvial gravel; tufa; pool; colluvial; alluvial	Flint	Pointed (incl. crude forms); backed biface; cleaver; cordiform; ovate; sub-triangular	Denticulates; endscrapers; notches; scrapers; pebble tools; retouched flakes	Cagny-La-Garenne I (Cxb, Cxv, Lg, Lj & Ca assemblages); Cagny-La-Garenne II (13, 14 & J assemblages); Rue De Cagny (Series 3); La Celle; Barnham; Elveden; Beeches Pit; Swanscombe (LMG & UMG); Hoxne (Upper & Lower Industries); Ferme de l'Epinette (MS assemblage); St-Pierre-lès-Elbeuf

Table 8: Summary table of early north-western biface sites, context, raw material, biface form and additional flake tool types (data from Moncel et al., 2015).

When looking at the early biface assemblages of north-west Europe (Table 8) it can be seen that there is a diversity of biface form within the assemblages and the sites tend to cluster around fluvial locations, often at the convergence of ecological zones (Table 6). This is perhaps not surprising as this pattern of hominin site location has been repeated throughout the Old World, probably reflecting the preference of hominins in exploiting a range of resources in the vein of the generalist (Grove, 2011; Potts, 2013). What is interesting is a pattern noticed by Moncel et al. (2015), that the early biface sites in north-west Europe tend to have a relatively low ratio of bifaces to other tools when compared to comparable sites in the Levant or Africa (although there are a few notable exceptions, e.g. Boxgrove). While there are taphonomic complications to this pattern (e.g. variable collecting histories), two potentially key trends have been highlighted (Moncel et al., 2015):

Firstly, the Early Middle Pleistocene sites (MIS 17-13) tend to have not only a range of biface forms made from both core and flake blanks, but they are also characterised by a range of raw material exploitations depending on local availability. This may indicate that the Early Middle Pleistocene biface makers were not locked into a single raw material but flexible enough in cognition and experience to work a range of lithologies when necessary. Alternatively, of course, it may equally suggest a limited ability for planning depth with a more immediate focus on utilising suitable raw materials as they occur in the local landscape. In addition, raw material seems to have differing impacts on the degree of shaping and size of bifaces present between southern British and northern French sites which may go some way to explaining the difference in artefact morphology. However, a common occurrence between these sites are the dual compositions of biface assemblages consisting of thick, crudely pointed bifaces with irregular cutting edges and more comprehensively worked bifaces with regular cutting edges and invasive removals.

Secondly, the late Middle Pleistocene (MIS 12-10) assemblages in contrast seem to be characterised by higher proportions of thinner bifaces with fine retouched edges, although overall shaping is still

varied within assemblages. Across the Table 8 sites large flakes could have been produced for blank production, but it would appear that few were. This may in turn reflect the suitability and increasing visibility of good flint sources in the landscape as well as reflect the hominins' ability to read and interpret the landscape around them. Another possible change during the late Middle Pleistocene in Europe (in contrast to the early Middle Pleistocene) is that the biface sites may be supported in the toolkit by a larger range of flake tool types (Table 8), although it is acknowledged that collection biases and varying typological schemes also complicate this interpretation.

Certainly, the patterns of hominin behaviour seen in the early biface sites of north-west Europe are diverse, but they tend to be explained in terms of the differences in local raw material and overall site function even if there are broad similarities in the shaping processes in biface manufacture (Moncel et al., 2015). We would suggest that these differences and similarities in biface shaping are probably more a consequence of local technological and functional decisions rather than cultural factors at this time.

Nonetheless the European biface package would also seem to suggest a range of additional technological developments – although it is not the position here that they are European innovations or that the biface per se enabled northern dispersals. Rather, it is the overall suggested behavioural package that may have facilitated the sustainable tipping point for hominin dispersal into north-west Europe. Preservation records are difficult for non-lithic technologies but there are preserved wooden spears from Clacton *c*. 400 kya (Warren, 1911) and spears and bone tools from Schöningen *c*. 300–337 kya (Richter and Krbetschek, 2015; Van Kolfschoten et al., 2015b). While recent palaeogenetic evidence raises the possibility that these artefacts may be the preserve of a later speciation event (Meyer et al., 2016a), the mosaic character of Middle Pleistocene hominin evolution combined with the Boxgrove puncture wound evidence supports a position that the early

biface makers of north-west Europe may have had an extensive lithic and non-lithic tool kit including spears.

In addition, hints of hide processing can be seen in the elaborate scrapers from High Lodge, Warren Hill, Brandon Fields and Maidscross Hill (Moncel et al., 2015) which would presumably indicate a possible use for them as clothing or shelter components. However, direct evidence for such behaviour is sadly lacking. It is also clear that the later biface-making hominins had the controlled use of fire from well-known sites such as Beeches Pit, Ménez Drégan and possibly Aroeira at *c*. 400 kya (Daura et al., 2017; Gowlett, 2006; Molines et al., 2005; Preece et al., 2006). Although some argue that these are isolated instances of controlled fire use in Europe (Roebroeks and Villa, 2011) they are supported by dates for controlled fire use in other parts of Old World since *c*. 800 kya at least (Goren-Inbar et al., 2004).

The biface itself has often been seen to represent something more than just a functional tool with explanations varying from butchery, mechanisms of sexual selection and aesthetic markers to cultural mediators and objects used to negotiate the landscapes and social-scapes of the Acheulean world (Gamble, 1998; Hopkinson and White, 2005; Kohn and Mithen, 1999; Machin et al., 2007; Machin and Mithen, 2004; McPherron, 2000; Porr, 2005; Saragusti et al., 1998; Wenban-Smith, 2004; White, 1998; Wynn, 1995). We agree with aspects of the above and emphasise again that it is not the biface per se that allowed hominins to have a more sustained presence in north-west Europe, but perhaps the full behavioural package that accompanied biface manufacture.

Why then did it take so long for biface makers to enter north-west Europe when there is clearly evidence for these artefacts stretching back to 1.7 million years ago in Africa (Diez-Martin et al., 2015) and first appearing in south-western Asia soon after (Pappu et al., 2011)? We suggest here that not only do you need the biface package (with all the social and technological benefits that

478 includes) but you also need a threshold level of behavioural plasticity that is tied to a brain size of
479 over 1100cm^3 at a sustained species level for hominin populations to persistently survive the
480 difficulties of the European north-west. Since Moncel et al. (2015) and Table 8 demonstrate that
481 bifaces are present in Europe from at least *c*. 700 kya, we suggest that this plasticity package must
482 have been present across the early/late Middle Pleistocene boundary (MIS 13/12).
483
484 **4. Conclusion**
485 Our interpretation of the palaeoenvironmental (life on the ground) and palaeoanthropological (life
486 history) records from north-western Europe across the *c*. 800-600kya period has struggled to find a
487 clear pattern of changing conditions before and after this 'boundary'. By contrast, the archaeological
488 evidence does highlight the appearance of the biface by *c*. 700kya, although it does not become
489 widespread until MIS 13. The status of this possible behavioural boundary is newly noteworthy in
490 light of the recent palaeo-genetic studies that have pushed back the date of the last common
491 ancestor between modern humans and Neanderthals to *c*. 700 kya (Meyer et al., 2016a). This makes
492 the apparent step-change in the European archaeological record ever more intriguing. Perhaps such
493 changes may simply relate to the appearance of a new species (*H. heidelbergensis?*) able to cope
494 with the rigours of the north-west, although it remains uncertain as to whether such a species is an
495 *in situ* development or a dispersal into Europe from elsewhere.
496
497 However, there may be a subtler and more nuanced pattern to the archaeological record, reflecting
498 a multi-phased hominin occupation of north-west Europe, which we dub here the 'punctuated long
499 chronology' (Table 9), which builds on the modified short chronology (Dennell and Roebroeks, 1996).
500 The first phase, contemporary with the pre-1 million year flake and core occupations of the southern
501 European zone exemplified by Dmanisi, Orce and Atapuerca, is characterised by northern absence.
502 Shortly after 1 million years ago there would appear to be small scale, fragmented dispersals of
503 hominins further north into cooler climates such as at Happisburgh III, equipped with a flake and

core lithic tool kit. This is succeeded by the appearance of biface-producing hominins between *c*. 700-500kya, possibly originating from regions outside Europe. These biface-makers had a varied lithic and organic tool kit, incorporating the behavioural plasticity package within a broad geographic range, but would still seem to be limited in terms of overall population numbers. This in turn may reflect the continuing challenges of a hominin population adapting to the unique conditions of Pleistocene north-west Europe. We suggest that this second phase of small-scale, biface-making populations, although important, has tended to be over-emphasised in interpretations of the north-west European Palaeolithic record due to the quality of preservation at occasional key sites such as Boxgrove. In contrast, we suggest here that the major behavioural change (the plasticity package) occurs at a species level, leading to demographic growth, during a third phase after MIS 12. This can tentatively be supported by the changing richness, and diversity in tool kits, of the artefactual record (e.g. the terrace archives of the Thames, Solent and Somme; Ashton and Hosfield, 2010; Ashton and Lewis, 2002; Tuffreau and Antoine, 1995) and evidence for cooler climate tolerances (e.g. Hoxne and Cagny-la-Garenne). Perhaps most tantalisingly, such a shift might also map onto the latest palaeogenetic timings for the origins of the early Neanderthals at around *c*. 430kya (Meyer et al., 2016a). Further evidence is certainly need to test this hypothesis, and we suggest an enhanced understanding of the quantities of artefacts at different periods, normalised with reference to sample biases and site taphonomy (e.g. Ashton and Hosfield, 2010; Ashton and Lewis, 2002), as one possible approach.

Phase	**1**	**2**	**3**	**4**
Summary	Only southern Europe occupied.	Continued occupation of southern Europe, with small-scale, fragmented dispersals into northern Europe (e.g. Happisburgh III).	Continued occupation of southern and northern Europe. Emerging behavioural plasticity package (possibly originating from outside Europe), but limited overall population numbers, especially in the north.	Full behavioural plasticity package and expanded population numbers across Europe.
Timeframe	**Before 1mya**	**c. 1mya-700kya**	**c. 700-500kya**	**c. 500-300kya**
Archaeological signature	Small assemblages (typically 10s and 100s of artefacts)	Small assemblages (typically 10s and 100s of artefacts)	Larger individual assemblages (100s and 1000s of artefacts)	Large assemblages (1000s and 10000s of artefacts), with multiple large sites
Context	Cave(?) and open-air sites	Cave(?) and open-air sites	Cave and open-air sites	Cave and open-air sites
Assemblage character	Flake and pebble tools, with potential organic tools	Flake and pebble tools, with potential organic tools	Bifaces and flake tools (limited range), with demonstrated	Bifaces and flake tools (expanded range), with demonstrated

			organic tools	organic tools
Human Remains	Very occasional	Occasional	Occasional	Occasional, but with abundant remains at individual sites

523

524 **Table 9**: A punctuated long chronology for the hominin occupation of Europe.

525

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